



Suppression of the N1 auditory evoked potential for sounds generated by the upper and lower limbs



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ABSTRACT

Sensory attenuation is typically observed for self-generated compared to externally generated action effects. In the present study we investigated whether auditory sensory suppression is modulated as a function of sounds being generated by the upper or lower limbs. We report sensory attenuation, as reflected in a reduced auditory N1 component, which was comparable for sounds generated by the lower and the upper limbs. Increasing temporal delays between actions and sounds did not modulate suppression of the N1 component, but did have an effect on the latency of the N1 component. In contrast, for the P2 component sensory suppression was only observed for sounds generated by the hands and presented at short latencies. These findings provide new insight into the functional and neural dynamics of sensory suppression and suggest the existence of comparable agency mechanisms for both the upper and the lower limbs.

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1. Introduction

Imagine yourself walking down a dark street at night. When hearing footsteps, it would be important to determine whether these sounds correspond to your own footsteps, or whether these sounds are generated by someone else. As this example illustrates, an important mechanism underlying our everyday actions is the ability to determine whether a specific action-effect is related to our own actions or not. The *feeling of agency* has been defined as ‘the sense that I am the one who is causing or generating an action’ (Gallagher, 2000). The feeling of agency is crucial for distinguishing self-generated actions from actions generated by others. As such the neurocognitive mechanisms underlying the feeling of agency may support self-other distinction and may contribute to the subjective feeling of self-awareness (de Vignemont & Fournieret, 2004; Gallagher, 2000; Pacherie, 2008).

In the last two decades many studies have investigated the functional and neural mechanisms underlying the feeling of agency (for review, see: David, Newen, & Vogeley, 2008; de Vignemont

& Fournieret, 2004; Kuhn, Brass, & Haggard, 2012). A prominent model proposed that the feeling of agency relies on the successful integration of predicted and observed action effects through the use of an internal forward model (Blakemore, Wolpert, & Frith, 2000; Frith, 2005). According to internal forward models of motor control, the brain uses efferent signals from motor-related and/or somatosensory areas to anticipate the sensory consequences of our movements (Wolpert, 1997). The feeling of agency is typically studied by introducing visuo-spatial or temporal deviations between observed and actual movements (Fournieret & Jeannerod, 1998; Franck et al., 2001; Kannape & Blanke, 2012; Kannape, Schwabe, Tadi, & Blanke, 2010; R Salomon, Lim, Kannape, Llobera, & Blanke, 2013; van den Bos & Jeannerod, 2002). It has been found for instance, that small visuo-spatial angular deviations result in an online automatic correction of ongoing movements, that often happens outside awareness (e.g. Fournieret & Jeannerod, 1998). However, with increased deviations between actual and observed movements the feeling of agency typically decreases and participants deliberately try to correct their movements to adjust the perturbation. Similarly, it has been shown that with increased temporal mismatches between executed and felt touches (applied to one’s own body), the sensation of ticklishness increases and it has been argued that this is due to the increased difficulty to anticipate the touch (e.g. Blakemore, Frith, & Wolpert, 1999). It has also been suggested that hallucinations in schizophrenia may be related to

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an impaired internal forward model, resulting in the feeling that self-generated sensations and experiences are actually generated by someone else (Frith, 2005).

The anticipation of the consequences of one's movements has been associated with sensory suppression for self-generated action effects. For instance, self-generated touch is perceived as less intense than externally generated identical tactile stimuli (Blakemore et al., 2000) and is associated with reduced activation in somatosensory areas (Blakemore, Wolpert, & Frith, 1998). Similarly, self-generated sounds and self-generated light flashes are perceived as less intense and are associated with reduced sensory evoked brain responses (for review, see: Hughes, Desantis, & Waszak, 2012; Hughes & Waszak, 2011). Animal studies have shown a reduced responsiveness of neurons in the auditory cortex during vocalization (Eliades & Wang, 2003; Muller-Preuss & Ploog, 1981). Similar findings have been reported in humans based on intracranial electrode recordings from the auditory cortex during self-produced speech (Creutzfeldt, Ojemann, & Lettich, 1989). Sensory suppression is strongest for unchanged self-produced speech sounds, but is greatly reduced when auditory feedback is altered (e.g. pitch-shifted sounds; cf. Chen et al., 2012; Christoffels, van de Ven, Waldorp, Formisano, & Schiller, 2011; Heinks-Maldonado, Mathalon, Gray, & Ford, 2005; Martikainen, Kaneko, & Hari, 2005). In all these cases, efferent information is used to anticipate the sensory consequences of one's actions, which results in reduced activation of sensory brain areas for self-generated sounds compared to externally generated sounds (but see: R. Salomon, Szpiro-Grinberg, & Lamy, 2011).

A well-established neural marker of sensory suppression in the auditory domain is the reduction of the auditory N1 component in the electroencephalogram (EEG) that is typically observed in association with the processing of self-generated compared to externally generated sounds or visual events (Baess, Horvath, Jacobsen, & Schroger, 2011; Baess, Jacobsen, & Schroger, 2008; Chen et al., 2012; Gentsch, Kathmann, & Schutz-Bosbach, 2012; Gentsch & Schutz-Bosbach, 2011; Martikainen et al., 2005; Sowman, Kuusik, & Johnson, 2012; Stekelenburg & Vroomen, 2012). In a typical auditory suppression paradigm, participants are instructed to press a button at a regular interval and in 'motor + auditory' blocks, each button press is accompanied by the presentation of an auditory stimulus. In 'auditory-only' blocks, the same sequence of sounds is presented, but the sounds are generated externally while the subject does not move. In the 'motor-only' condition, the participant presses a button but no sounds are presented. In the ERP (event-related potential) analysis the 'motor-only' condition is often subtracted from the 'motor + auditory' condition to control for movement-related effects. Typically, auditory suppression is reflected in a reduced N1 (and often a P2) component for self-generated sounds during the 'motor + auditory' condition compared to externally presented sounds in the 'auditory-only' blocks (Baess et al., 2011; Baess, Widmann, Roye, Schroger, & Jacobsen, 2009). In a recent study it was found that patients with focal cerebellar lesions showed a reduced sensory suppression for self-generated sounds (Knolle, Schroger, Baess, & Kotz, 2012). Given the importance of the cerebellum in supporting internal forward models of motor control (Miall, 1998), this finding substantiates the interpretation that auditory suppression reflects a predictive process. More specifically, it is argued that the brain anticipates upcoming sounds based on efferent signals related to the motor commands, which results in a reduced auditory response to anticipated compared to unanticipated stimuli (Bendixen, SanMiguel, & Schroger, 2012; Hughes & Waszak, 2011).

Several studies have focused on the different factors that may influence sensory suppression and on several potential confounds that could underlie the effects observed. An obvious concern is that the reduced auditory responses during self-generated sounds

are related to increased arousal during preparatory motor processes. However, sensory suppression has also been observed when self-produced and externally generated sounds were intermixed within the same block, thereby making an arousal explanation less likely (Baess et al., 2011; Knolle, Schroger, & Kotz, 2013). A related concern is that auditory suppression may be related to attentional differences, as early EEG studies have shown that the amplitude of the N1 component is enhanced for attended compared to unattended stimuli (Hillyard, Hink, Schwent, & Picton, 1973). For instance, in a recent study it was found that mechanical impact (i.e. receiving somatosensory feedback from touching a button) has a substantial effect on sensory suppression – possibly through a process whereby attention is directed away from the auditory stream (Horvath, 2014). However, several studies have controlled for the potential confound that attentional effects could underlie sensory suppression (i.e. by manipulating participants' level of attention to the auditory stream) and it was found that sensory suppression is automatic and independent of attention (Saupe, Widmann, Trujillo-Barreto, & Schroger, 2013; Timm, SanMiguel, Saupe, & Schroger, 2013). Other studies have controlled for the effects of temporal predictability, for instance by using different temporal delays between the action and the sound and by introducing externally cued sounds (Horvath, Maess, Baess, & Toth, 2012; Lange, 2011; Sowman et al., 2012). It has been found for instance that N1 suppression decreases with longer stimulus-onset asynchronies (SOAs), whereas P2 suppression was unaffected by the temporal delay (SanMiguel, Todd, & Schroger, 2013). Furthermore, temporal cueing of sounds resulted in a similar suppression of the auditory P2 component as observed for self-generated sounds (Sowman et al., 2012), indicating that sensory suppression may be partly related to effects of temporal predictability.

Most studies on agency and sensory attenuation have focused selectively on actions involving the upper limbs, by introducing visuo-spatial or temporal mismatches between executed and observed hand actions (Fournieret & Jeannerod, 1998; Franck et al., 2001; van den Bos & Jeannerod, 2002) or by presenting sounds in association with hand button presses (for review, see: Hughes, Desantis, & Waszak, 2013). However, as the example from the introduction illustrates, many of our everyday actions involve other body parts than the upper extremities alone. For instance, we walk, run, swim, jump, kick and each of these actions involves the entire body. It has been suggested that a fundamental aspect of bodily consciousness is that we experience the self as a single coherent representation of the spatially situated body (Blanke & Metzinger, 2009). Recent studies have shown that this sense of self and the perceived self-location can be experimentally manipulated, by inducing visual-tactile or visual-proprioceptive conflicts (Aspell, Lenggenhager, & Blanke, 2009; Blanke, 2012; Ionta et al., 2011; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). Interestingly, it has also been shown that people show only limited awareness of their body location during locomotion (Kannape et al., 2010), indicating a similar dissociation between the feeling of agency and the actual bodily movements as observed for hand movements (Fournieret & Jeannerod, 1998). In another study it was found that increased temporal mismatches between one's actual footsteps and experimentally introduced footstep sounds resulted in a decreased feeling of agency and a slower gait cycle (Menzer et al., 2010), also comparable to the effects observed for hand movements (Leube, Knoblich, Erb, & Kircher, 2003). Similarly, visual feedback presented with a temporal delay also resulted in a decrease in the feeling of agency and systematically modulated the gait cycle (Kannape & Blanke, 2013). These findings are compatible with the view that planning actions with both the upper and the lower limbs relies on the use of an internal forward model involving an efferent copy, which is used to anticipate the sensory consequences of one's actions (see for instance: Yavari, Towhidkhal, & Ahmadi-Pajouh, 2013).

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